Observations of Interspecific Amplexus Between Western North American Ranid Frogs and the Introduced American Bullfrog (Rana catesbeiana) and an Hypothesis Concerning Breeding Interference

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ABSTRACT.—Introduced American bullfrogs (*Rana catesbeiana*) come in contact with native amphibians on four continents and are well established in lowlands of western North America. To date, research on the effects of introduced bullfrogs on native frogs has focused on competition and predation, and is based largely on larval interactions. We present observations of interspecific amplexus between bullfrogs and two native ranid frogs (*R. aurora* and *R. pretiosa*) from six sites across the Pacific Northwest that imply that this interaction is more widespread than currently recognized. Our observations indicate that *R. catesbeiana* juveniles and subadults in this region are of appropriate size to elicit marked amplectic responses from males of both native species. Our literature review suggests that greater opportunity may exist for pairings between *R. catesbeiana* and native *R. aurora* or *R. pretiosa* than among syntopic native ranids in western North America. We hypothesize that interspecific amplexus with introduced *R. catesbeiana* could result in reproductive interference with negative demographic consequences in native ranid populations that have been reduced or altered by other stressors.

INTRODUCTION

Accelerating human-assisted introductions continue to redistribute species beyond their native ranges and bring formerly allopatric species into contact (Elton, 1958; Vitousek *et al.*, 1996: Mack *et al.*, 2000). The American bullfrog (*Rana catesbeiana*) is among the dramatic examples of this pattern. *Rana catesbeiana* is native to much of eastern North America (Wright and Wright, 1949; Conant and Collins, 1991). As a result of human introductions,

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R. catesbeiana is established in parts of the Caribbean (Mahon and Aiken, 1977), Europe (Lanza, 1962; Stumpel, 1992), Japan (Telford, 1960) and Latin America (Flores-Nava, 2000), and is now common in many lowland areas of western North America (Bury and Whelan, 1984; Jennings and Hayes, 1985; Richter and Azous, 1995). Introduced *R. catesbeiana* can impact native ranid frogs directly through competition and predation (Kupferberg, 1997; Lawler *et al.*, 1999; Pearl *et al.*, 2004) and indirectly by increasing native species' susceptibility to other predators (Kiesecker and Blaustein, 1998). Hence, the expansion of *R. catesbeiana* within its introduced range and concurrent losses of native anurans have generated concern about the role of *R. catesbeiana* in amphibian declines in western North America (*e.g.*, Hayes and Jennings, 1986; Doubledee *et al.*, 2003).

To date, research on the effects of *Rana catesbeiana* on native amphibians has focused strongly on larval interactions (Kupferberg, 1997; Kiesecker and Blaustein, 1998; Lawler *et al.*, 1999; Adams, 2000; Kiesecker *et al.*, 2001; but see Pearl *et al.*, 2004). One uninvestigated interaction is the potential for breeding interference between adult native ranid frogs and introduced *R. catesbeiana*. High adult fecundity and larval survivorship often result in high densities of juvenile *R. catesbeiana* in their introduced western range (Cohen and Howard, 1958; MPH and CAP, *unpubl. data*). Many western ranids (including *R. aurora* and *R. pretiosa*) are explosive breeders, often completing oviposition in fewer than 7–14 d in early spring (Storm, 1960; Licht, 1969 a, b). Available data suggest *R. aurora* and *R. pretiosa* exhibit prolonged amplexus relative to their abbreviated breeding seasons (Licht, 1969a; Nussbaum *et al.*, 1983), a mate-guarding behavior associated with many explosive breeding ranids (Wells, 1977; Howard, 1980). In the absence of other behavioral isolating mechanisms, potential exists for male native ranids to amplex with young *R. catesbeiana* rather than female conspecifics. Any negative population effects of interspecific pairings are of particular concern for *R. pretiosa*, which is extirpated from >70% of its historic range and rarely persists with *R. catesbeiana* (Hayes, 1997; Pearl *et al.*, 2004).

Here, we present observations of interspecific amplexus between introduced *Rana catesbeiana* and the native western North American ranid frogs, *R. aurora* and *R. pretiosa*, to suggest an uninvestigated but potentially direct, non-predatory impact of introduced *R. catesbeiana*: reproductive interference. We compile published observations of interspecific amplexus involving native ranids in western North America to develop a basis for proposing this hypothesis and suggest conditions under which the negative demographic effects of reproductive interference might be expected.

METHODS AND SITE DESCRIPTIONS

With one exception (a *Rana pretiosa–R. catesbeiana* pair from Crosswater, Oregon, that preceded *R. pretiosa* breeding by about 10 wks), all our observations of interspecific amplexus were made at native ranid reproductive sites during the breeding interval for the native frog species. Eight of our 18 *R. pretiosa–R. catesbeiana* pairings and three of four *R. aurora–R. catesbeiana* pairings were of free-ranging frogs within breeding habitat used by the native species (Table 1). We made our observations of free-ranging frogs during visual surveys for native ranid egg masses or reproductive activity. The remaining observations (nine *R. pretiosa–R. catesbeiana* and one *R. aurora–R. catesbeiana* pairings) were of frogs captured in submerged crayfish traps. Traps were set within 130 m of *R. pretiosa* breeding sites in water 9–80 cm deep. We checked traps every 1–2 d. With one exception [Ankeny National Wildlife Refuge, Oregon (ANWR)], all observation sites support breeding pop-ulations of *R. catesbeiana* and at least one of *R. aurora* or *R. pretiosa*. The site at ANWR is a small temporary pond where *R. aurora* breed, but *R. catesbeiana* do not; *R. catesbeiana* breed

TABLE 1.—Observations of interspecific amplexus between native ranid frogs and introduced bullfrogs in northwestern North America. The clasping (upper) frog is listed first for each pair. Length is to nearest 1 mm; mass is to nearest 1 g. (−) is data lacking. Localities are by State/Province, County (in US), Site

Species	Sex	Length	Mass	Locality[a]	Date
R. pretiosa	Male	63	25	OR, Deschutes, Crosswater	14 Jan. 2002
R. catesbeiana[b]	Juvenile	73	—		
R. pretiosa	Male	57	18	OR, Deschutes, Crosswater	20 Mar. 2003
R. catesbeiana[b]	Juvenile	64	—		
R. pretiosa	Male	56	16	OR, Deschutes, Crosswater	18 Mar. 2004
R. catesbeiana[b]	Juvenile	60	21		
R. pretiosa	Male	58	18	WA, Klickitat, CLNWR	20 Mar. 1997
R. catesbeiana	Female	69	26		
R. pretiosa	Male	63	21	WA, Klickitat, CLNWR	25 Mar. 1997
R. catesbeiana	Female	73	33		
R. pretiosa	Male	65	28	WA, Klickitat, CLNWR	13 Mar. 1998
R. pretiosa	Male	65	27		
R. pretiosa	Male	62	23		
R. pretiosa	—	—	—		
R. pretiosa	—	—	—		
R. catesbeiana	Female	105	115		
R. pretiosa	Male	55	16	BC, MDA	07 Mar. 2000
R. catesbeiana[b,c]	Juvenile	61	32		
R. pretiosa	Male	54	16	BC, MDA	07 Mar. 2000
R. catesbeiana[b,c]	Juvenile	52	29		
R. pretiosa	Male	55	16	BC, MDA	05 Apr. 2001
R. catesbeiana[b,c]	Juvenile	46	25		
R. pretiosa	Male	59	20	BC, MDA	14 Apr. 2002
R. catesbeiana[b,c]	Juvenile	62	37		
R. pretiosa	Male	50	12	BC, MDA	15 Apr. 2002
R. catesbeiana[b,c]	Juvenile	60	34		
R. pretiosa	Male	64	23	BC, MDA	04 Apr. 2003
R. catesbeiana[b,c]	Female	67	52		
R. pretiosa	Male	45	13	BC, MDA	09 Apr. 2003
R. catesbeiana[b,c]	Juvenile	58	36		
R. aurora	Male	62	—	OR, Marion, ANWR	27 Feb. 2003
R. catesbeiana	Female	84	—		
R. aurora	Male	59	19	OR, Multnomah, Burlington Bottoms	25 Feb. 1998
R. catesbeiana	Female	81	42		
R. aurora	Male	56	16	OR, Multnomah, Sandy River Delta	22 Feb. 1997
R. catesbeiana	Male	74	32		
R. aurora	Male	51	15	BC, MDA	03 Mar. 2000
R. catesbeiana[b,c]	Female	65	38		

[a] State/Provinces are British Columbia (BC), California (CA), Oregon (OR) and Washington (WA). Site abbreviations are in METHODS AND SITE DESCRIPTIONS

[b] Pair found in submerged crayfish trap

[c] Bullfrog deceased

[d] Table excludes 5 *Rana pretiosa–R. catesbeiana* pairs for which we lack size measurements: 4 pairs from CLNWR (20, 25 Mar. 1997 and 13, 14 Mar. 1998; all free-ranging frogs; 1 *R. catesbeiana* near death, other 3 alive) and 1 pair from MDA (09 Mar. 2000; captured in trap; *R. catesbeiana* alive)

in a permanent pond ca. 0.3 km away. Two sites [Maintenance Detachment Aldergrove, British Columbia (MDA) and Conboy Lake National Wildlife Refuge, Washington (CLNWR)] support breeding populations of *R. catesbeiana, R. aurora* and *R. pretiosa.*

We measured size [snout-vent length (SVL)] of captured frogs to the nearest mm, and mass to the nearest gram. For *Rana pretiosa–R. catesbeiana* partners, we used a Wilcoxon signed-rank test with corrections for ties (S-Plus 2000, MathSoft, Inc.) to compare SVL and mass of clasping (upper) and clasped (lower) frogs. We used a one-tailed test because breeding males are usually smaller than breeding females in western ranids, including *R. aurora* and *R. pretiosa* (Licht, 1969b, 1975; Nussbaum *et al.*, 1983). We excluded SVL and mass data from the multiple-male *R. pretiosa*–single *R. catesbeiana* amplectic group as we were unable to measure all attendant *R. pretiosa*. Due to small sample size, we did not statistically compare partner sizes for *R. aurora–R. catesbeiana* pairs. Mean frog SVL and mass are expressed as $\bar{x} \pm 1$ SD.

<center>RESULTS</center>

<center>*RANA PRETIOSA–RANA CATESBEIANA* PAIRINGS</center>

We made 18 observations of *Rana pretiosa–R. catesbeiana* amplexus at one site each in southwestern British Columbia (MDA; $n = 8$ pairs; Table 1), central Washington (CLNWR; $n = 7$) and central Oregon (Crosswater; $n = 3$). In every case, the clasping partner or partners were *R. pretiosa*. In one case at CLNWR, we recorded five *R. pretiosa* clasping partners. All identified clasping partners ($n = 16$) were male *R. pretiosa*. Except for one subadult (105 mm SVL) female *R. catesbeiana*, all partners being clasped were juvenile *R. catesbeiana* < 80 mm SVL. Based on SVL, partners being clasped were significantly larger than their clasping partners ($Z = -2.397$, P $= 0.008$, $n = 12$). Partners being clasped averaged 5.5 ± 6.2 mm longer than clasping partners (*R. catesbeiana* being clasped $\bar{x}_{SVL} = 62.1 \pm 8.0$ mm, range: 46–73 mm; clasping *R. pretiosa* $\bar{x}_{SVL} = 56.6 \pm 5.5$ mm, range: 45–64 mm). Only two juvenile *R. catesbeiana* (both from MDA) were shorter then their clasping partners. Based on mass, partners being clasped were also significantly larger than their clasping partners ($Z = -2.752$, P $= 0.003$, $n = 10$), averaging 15.4 ± 7.5 g heavier than their clasping partners (*R. catesbeiana* being clasped $\bar{x}_{Mass} = 32.5 \pm 8.6$ g, range: 21–52 g; clasping *R. pretiosa* $\bar{x}_{Mass} = 17.1 \pm 3.4$ g, range: 12–23 g).

Seven of the eight *Rana catesbeiana* in interspecific pairings with *R. pretiosa* from MDA were dead. One of three *R. catesbeiana* from *R. pretiosa* pairings (the free-swimming pair) at Crosswater was also dead. We observed no bloating or fungal growth typical of older carcasses on any dead *R. catesbeiana*. One of the seven *R. catesbeiana* at CLNWR was moribund and seemed near death; the other six were alive, seemingly healthy. All *R. pretiosa* clasping partners appeared to be in good condition.

<center>*RANA AURORA–RANA CATESBEIANA* PAIRINGS</center>

We report new observations of *Rana aurora–R. catesbeiana* amplexus ($n = 1$ pair at each site) from three sites in western Oregon and one in southwestern British Columbia (Table 1). The clasping partner was a male *R. aurora* in all four cases. The partners being clasped were all juvenile *R. catesbeiana* <85 mm SVL and were uniformly longer and heavier than their clasping partner. Based on SVL, partners being clasped averaged 19.0 ± 3.8 mm longer than their clasping partners (*R. catesbeiana* being clasped $\bar{x}_{SVL} = 76.0 \pm 8.4$ mm, range: 65–84 mm; clasping *R. aurora* $\bar{x}_{SVL} = 57.0 \pm 4.7$ mm, range: 51–62 mm; $n = 4$). Based on mass, partners being clasped averaged 20.6 ± 4.0 g heavier than their clasping partners

(*R. catesbeiana* being clasped $\bar{x}_{\text{Mass}} = 37.3 \pm 5.0$ g, range: 32–42 g; clasping *R. aurora* $\bar{x}_{\text{Mass}} = 16.7 \pm 2.1$ g, range: 15–19 g; $n = 3$).

One of the four *Rana catesbeiana* paired with *R. aurora* (MDA) was dead, but lacked fungus and was not bloated. All clasping *R. aurora* appeared to be in good condition.

DISCUSSION

Confirmation of interspecific amplexus in anurans through direct field observations or genetic analysis of field-captured individuals is generally sparse (but *see* Green, 1985 and single cases listed below). Our observations confirm the occurrence of interspecific amplexus between each of two native ranids, *Rana aurora* and *R. pretiosa*, and introduced *R. catesbeiana*, and suggest that this behavior is geographically more widespread than previously recognized. We report the first observations of *R. pretiosa*–*R. catesbeiana* pairings. Single *R. aurora*–*R. catesbeiana* pairs have been reported from western Oregon (Storm, 1952) and southwestern British Columbia (Orchard, 1999). The only other reports of amplexus between native western ranids and introduced *R. catesbeiana* are those of Lind *et al.* (2003), who observed two cases of *R. boylii*–*R. catesbeiana* pairings from California. Reports of other interspecific pairings among ranid frogs in western North America are limited to four cases involving native species: *R. aurora* (male)–*R. pretiosa* (female; Licht, 1969a), *R. luteiventris*–*R. pipiens* (Ross *et al.*, 1994), *R. cascadae*–*Bufo boreas* (Brodie, 1968) and *B. boreas*–*R. aurora* (Brown, 1977). Collectively, the paucity of observations implies that less restriction may exist on pairings between *R. catesbeiana* and native *R. aurora* or *R. pretiosa* than among syntopic native ranids in western North America.

Size differences may contribute to reproductive isolation among other syntopic anurans (Blair, 1941; Mecham, 1961). However, our observations confirm that juvenile and young adult *Rana catesbeiana* in the Pacific Northwest are of the appropriate size to elicit amplexus from native male *R. aurora* and *R. pretiosa*. *Rana catesbeiana* observed in amplexus with native frogs in this study (46–105 mm) are similar in size to sympatric adult female *R. aurora* and *R. pretiosa* (55–96 mm; Licht, 1974; Nussbaum *et al.*, 1983). The frequency of juvenile and young adult *R. catesbeiana* in amplexus (all observations for which we were able to measure *R. catesbeiana*) may reflect a particularly suitable size of those younger age classes, their earlier seasonal emergence than adults (Willis *et al.*, 1956), or both. In the Pacific Northwest and California, *R. catesbeiana* generally transform at 35–55 mm after spending 0–2 winters as larvae and can reach 70–75 mm by the end of their first summer (Cohen and Howard, 1958; JB and CAP, pers. obs.). The impressive abundance of *R. catesbeiana* in lowland breeding sites within the range of *R. pretiosa* and *R. aurora* is of particular concern because availability of conspecifics relative to heterospecifics has been shown to affect conspecific amplexus frequency and reproductive success among syntopic native ranids (Hettyey and Pearman, 2003).

Prolonged amplexus in explosive-breeding anuran males is likely to represent one type of mate-guarding behavior, and may increase the likelihood that the male will reproduce successfully with conspecific females (Wells, 1977). Selection for mate-guarding is thought to be strong in species with breeding systems where availability of females is brief and competition for mates among males is high (Parker, 1974; Wells, 1977). *Rana aurora* and *R. pretiosa* appear to fit this pattern of prolonged amplexus within their abbreviated breeding seasons. For example, in spring 2004, we held 22 *R. pretiosa* pairs in traps at oviposition sites within 10 km of Crosswater. We checked traps every 1–2 d; frogs in traps were individually marked or weighed and were reexamined at the conclusion of the experiment. These *R. pretiosa* maintained amplexus for an average of 4.9 d (from placement in traps to oviposition date), and 1 pair remained in amplexus for 14 d before oviposition (JB and CAP, pers. obs.).

Most (>75%) of these pairs were in amplexus when we first intercepted them moving toward breeding sites, so these data conservatively estimate amplectic duration. Similarly, the single field-captured *R. aurora* (male)–*R. pretiosa* (female) pair reported by Licht (1969a) remained in amplexus for >3 d in the lab. Another field-caught *R. aurora* male, despite separation from its *R. catesbeiana* partner during transit, resumed and maintained amplexus in the lab for >3 d (Storm, 1952). Extended amplexus has also been documented in *R. luteiventris* (the sister taxon of *R. pretiosa*; Green *et al.*, 1996), including field-collected pairs that remained in amplexus for 4 d (Svihla, 1935) and 6.5 d (Turner, 1958) in the laboratory.

Amplectic grip strength of male *Rana aurora* and *R. pretiosa* is appreciable, and once paired, males do not readily relinquish partners (Licht, 1969a, b; Nussbaum *et al.*, 1983). Female *R. aurora* and *R. pretiosa* often have abrasions and scarring behind their arms as a result of the clasping of amplectic males (Storm, 1952; JB, RDH, MPH and CAP, pers. obs.). One *R. catesbeiana* clasped by a male *R. aurora* had 3-mm pectoral abrasions that had "penetrated to subdermal muscle" (Storm, 1952; p. 108). Wells (1977; p. 672) noted that "selection for female guarding probably also explains the tenacity of males holding onto dead females, bits of floating debris, and other inappropriate objects". Male *R. aurora* have been found in amplexus with apples and salamanders (Storm, 1960; Nussbaum *et al.*, 1983), and males of both native species will vigorously clasp rulers and observers' digits before and during the breeding season (JB, RDH, MPH and CAP, pers. obs.).

The exceptional grip strength of male *Rana aurora* and *R. pretiosa* may be linked to the high proportion of dead *R. catesbeiana* in our observations. Other factors potentially linked with the high proportion of dead *R. catesbeiana* include weakened condition upon emergence from overwintering, or that sexually immature *R. catesbeiana* (a prolonged rather than an explosive breeding species; Wells, 1977; Howard, 1978) may be less able to carry a clasping partner for extended periods without energetic costs. Eight of the 10 dead or moribund *R. catesbeiana* in amplexus with both native ranids were in traps, so it is also possible that trapping was related to mortality of clasped *R. catesbeiana.*

We hypothesize that reduced or demographically altered populations of explosive-breeding native ranids that co-occur with sizeable *Rana catesbeiana* populations are most likely to be affected by reproductive interference via interspecific amplexus. Our observations suggest that the presence of introduced *R. catesbeiana* has potential to reduce numbers of native male ranids available to couple with conspecifics during their abbreviated breeding periods. Direct reproductive interference would result if amplectic pairings were of sufficient frequency and duration to remove male natives from the local breeding pool. Some large breeding populations of western ranids, including *R. aurora*, appear to be strongly male-biased (Briggs and Storm, 1970; Calef, 1973). Ecologically relevant interference may be rare in native ranid populations with an abundance of breeding males. However, *R. pretiosa* populations that were considered female-biased or gender-balanced have been reported from British Columbia (Licht, 1974) and Washington (McAllister *et al.*, 2004), respectively. All else being equal, relatively fewer males in the latter population types should increase the potential for interspecific amplexus and breeding interference with negative demographic consequences. In addition, other interactions between native ranids and *R. catesbeiana*, as well as between native ranids and introduced warmwater fish (frequently associated with bullfrogs in modified western wetlands; Adams *et al.*, 2003), are likely to alter native population size and demographics (Licht, 1974; Kiesecker and Blaustein, 1998; Lawler *et al.*, 1999). Data on the frequency of interspecific amplexus relative to intraspecific breeding are needed to clarify the potential for reproductive interference as *R. catesbeiana* continue to expand their non-native range worldwide.

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